ENDEMISM IN THE WEST GULF COASTAL PLAIN: IMPORTANCE OF XERIC HABITATS

Michael H. MacRoberts

Bog Research
740 Columbia
Shreveport, LA 71104, U.S.A.
and Herbarium
Museum of Life Sciences
Louisiana State University in Shreveport
Shreveport, LA 71115, U.S.A.

Barbara R. MacRoberts

Bog Research
740 Columbia
Shreveport, LA 71104, U.S.A.
and Herbarium
Museum of Life Sciences
Louisiana State University in Shreveport
Shreveport, LA 71115, U.S.A.

Bruce A. Sorrie

3076 Niagara-Carthage Road
Whispering Pines, NC 28327, U.S.A

Robert E. Evans

NatureServe
6114 Fayetteville Road
Durham, NC 27713, U.S.A.

ABSTRACT

We studied the relationship between West Gulf Coastal Plain plant endemics and habitat. Approximately half of all West Gulf Coastal Plain endemics are associates of one habitat: xeric sandylands. We discuss some implications of these data to age and former extent of xeric sandylands in the region, notably isolation of the West Gulf Coastal Plain from the East Gulf Coastal Plain and a long and distinctive biotic history.

KEY WORDS: West Gulf Coastal Plain, endemic plants, grossarenic dry uplands, xeric sandylands.

RESUMEN

Se han estudiado las relaciones entre las plantas endémicas y el hábitat de la llanura costera del Golfo Oeste. Aproximadamente la mitad de los endemismo están asociados a un hábitat: terrenos arenosos xéricos. Se discuten algunas implicaciones de estos datos con la edad y extensión anterior de los terrenos arenosos xéricos en la región, notablemente aislamiento de la llanura costera del Golfo Oeste de la llanura costera del Golfo Este y una historia biótica larga y diferente.

INTRODUCTION

The Atlantic and Gulf Coastal plains have been recognized as a floristic province of distinction in part due to the high number of endemic and near-endemic species (Takhtajan 1986). In North America, the Atlantic and Gulf Coastal floristic province is second only to the California floristic province in endemics; approximately 27 percent of its native species are endemic or near endemic to it while in the latter province 48% are endemic or near endemic (Sorrie & Weakley 2001). While important local centers of endemism, such as the Apalachicola and Lake Wales regions of Florida, are well known, the significance of the West Gulf Coastal Plain (WGCP) has received almost no attention in the published literature or has been portrayed as largely depauperate in endemics (Ricketts et al. 1999). That the WGCP constitutes a regional center of endemism has been only recently demonstrated (Estill & Cruzan 2001; Sorrie & Weakley 2001). In this paper, based on a list of endemics from the WGCP and their habitat affiliation, we begin a dialogue about evolutionary origin, divergence, and migration for the region.

The WGCP center of endemism encompasses most of eastern Texas and western Louisiana, southern Arkansas, and southeastern Oklahoma (Fig. 1). Its western margin is not clearly defined, either geologically or botanically (Fennemen 1938; Christensen 2000). Its eastern boundary is the Mississippi River floodplain. Our definition is approximately the same as that of Sorrie and Weakley (2001) except that we encompass slightly more of south-central Texas because the east Texas flora clearly extends into those counties just east of Austin and San Antonio (Region 3 of Hatch et al. 1990). Although within the geological coastal plain, the gulf prairies and marshes (Region 2 of Hatch et al. 1990) are excluded because it appears that this region is a separate center of endemism (Sorrie & Weakley 2001), which itself needs detailed study.

METHODS

To develop a list of endemics, we obtained species distributional data from a wide variety of sources, including regional, state and local floras, floristic atlases, published papers, and monographs (among which are Correll & Johnston 1970; Jones 1977; MacRoberts 1984, 1989; Poole & Riskind 1987; Smith 1988; Bridges & Orzell 1989; Taylor & Taylor 1989; Hatch et al. 1990; Isely 1990; Nixon & Kell 1993; Texas Organization for Endangered Species 1993; Thomas & Allen 1993–1998; Walker 1993; Texas Natural Heritage Program 1995a; Turner 1996; Nesom 1997; Diggs et al. 1999; Kartesz & Meacham 1999; Louisiana Natural Heritage Program 1999; Turner in press; and several web sites centering on the Flora of Texas Consortium), Natural Heritage Program databases, our own field work, and an examination of herbarium specimens, notably at ASTC, BRIT, Corpus Christi Museum of Science and History, GH, LSU, LSUS, NCU, NLU, SBSC, SHST, TAMU (on line), TEX, VDB, and WWF. The list was begun independently of Sorrie and Weakley (2001) and has continued to develop after their list appeared.

We consider those species to be endemic whose occurrence is limited to the WGCP; near-endemic refers to species that are at least 90 percent centered on the WGCP. These species are listed in Appendix 1.

We encountered two major problems in developing the list. First, distributional information is incomplete in many cases. Various state and regional distribution maps and descriptions are either incomplete or do not agree. Second, taxonomic difficulties are frequent: for example, should *Trillium texanum* Buckley be considered a species, a subspecies, or a distinct taxon at all? We simply have followed the predominant view where possible (e.g., Jones et al. 1997;

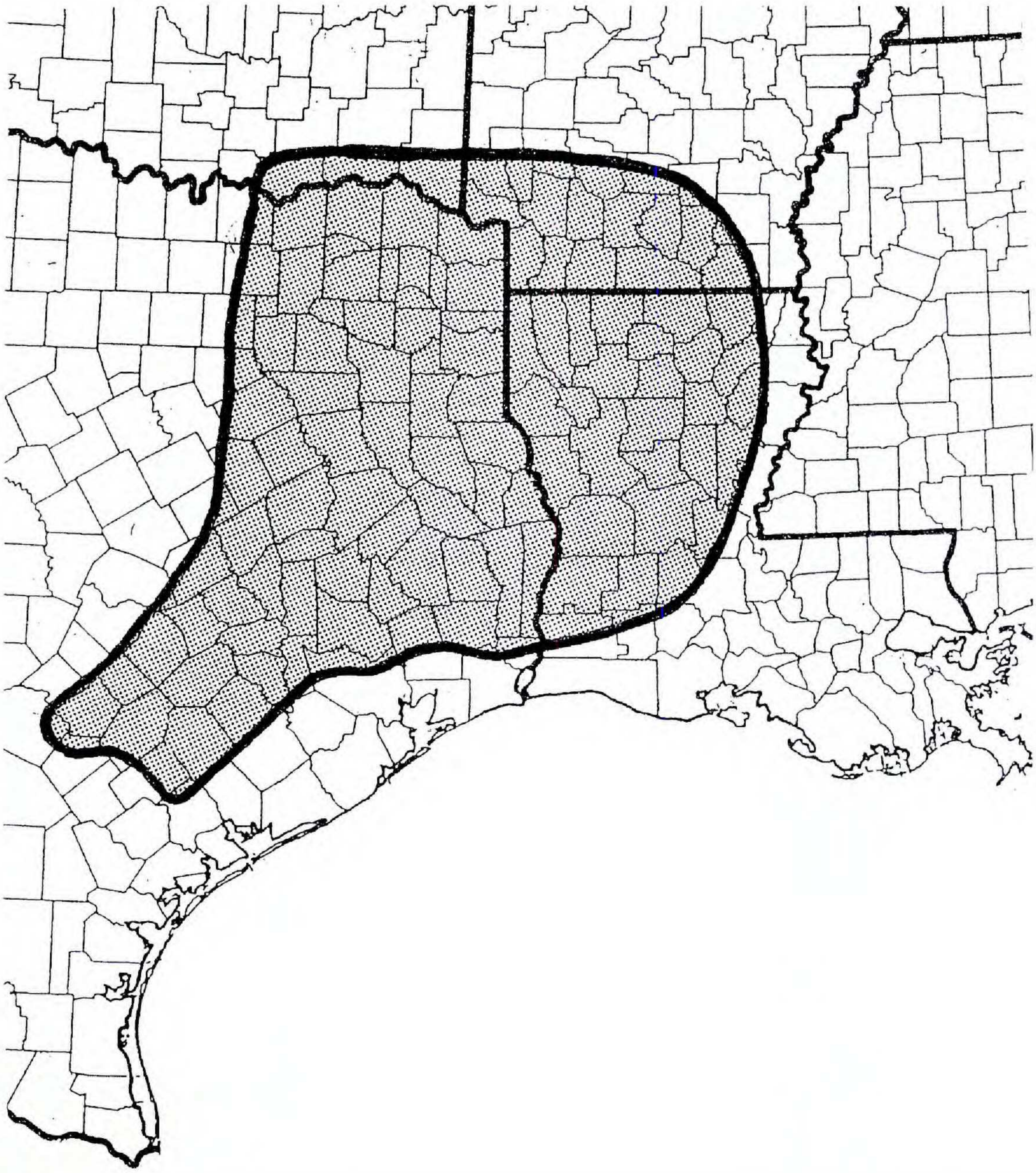

FIG. 1. Map showing West Gulf Coastal Plain.

Kartesz & Meacham 1999). We have developed a fairly conservative list, which we will continue to update and refine in future.

After we had developed the endemic/near-endemic list (which, for the sake of brevity, will be referred to hereafter as "endemics"), we attempted to determine for each taxon its community association (habitat) in the WGCP. We examined all major classifications (Diamond et al. 1987; Texas Organization for Endangered Species 1992; Harcombe et al. 1993; Foti et al. 1994; Texas Natural Heritage Program 1995b; Louisiana Natural Heritage Program 1998; Turner et.

al. 1999; Van Kley 1999a, 1999b; Weakley et al. 1999; Hoagland et al. 2000). We selected the Turner et al. (1999; see also Van Kley 1999a, 1999b) classification because it is based on quantitative data and is manageable and applicable over a wide geographic area. With a few modifications, it is presented in Appendix 2 with associated plant group in parentheses and with The Nature Conservancy (TNC) "ecological group" designations in brackets (Weakley et al. 1999). We then assigned each endemic to habitat of best fit on the basis of the literature, personal experience, and herbarium labels. It was not always possible to determine community type, a few taxa were assigned to two types, and a few were left blank.

RESULTS

Table 1 presents number and percent of WGCP endemics associated with each community. Of the 96 taxa in our endemic list, we were able to classify all but three to one or more communities. Number 1, xeric sandylands, proved to have by far the most endemics. Of the 96 endemics, 53 percent are associated with xeric sandylands. The communities with the next highest number of endemics are barrens, glades and weches, and bogs and wet pine savannas, each with nine percent of the total.

TABLE 1. Plant communities and number and percent of WGCP endemics associated with each.

Community	Number	Percent
1 Xeric sandylands	51	53
2 Upland pine savanna, mixed woods	4	4
3 Loamy dry-mesic uplands	0	0
4 Bogs, wet pine savannas	9	9
5 Calcareous forest	0.5	1
6 Mayhaw pond	2	2
7 Barrens, glades, weches barrens	9	9
8 Beech slopes	1	1
9 Stream course	1.5	2
10 Baygall	3.5	4
11 Bottomland, floodplain	6	6
12 Ponds, marshes	0	0
13 Prairies	5.5	6
Unknown	3	3
Total	**96**	**100**

DISCUSSION

Xeric sandylands have the most endemics, a fact recognized by Bridges and Orzell (1987, 1989) some years ago. Of the three genera endemic to the WGCP, *Maclura*, *Brazoria*, and *Rhododon*, two, *Brazoria* and *Rhododon*, are associated with xeric sandylands (Turner 1995, 1996). Xeric sandylands are open to sparsely wooded areas that typically occur on terraces or ridges composed of deep sand, generally of marine Tertiary origin (McBryde 1933; Bridges & Orzell 1989; Harcombe et al. 1993; MacRoberts & MacRoberts 1994, 1995, 1996; MacRoberts et al. 2002; Turner et al. 1999). Water and air move rapidly through these soils. Soils, where undisturbed, are often cryptogamic. Foliose lichens (*Cladonia* spp.) may be common. Stunted *Quercus stellata* Wangenh., *Q. margarettiae* Ashe ex Small, *Q. incana* W. Bartram, and various *Carya* species are dominant trees in xeric sandylands. Other characteristic species are *Bulbostylis ciliatifolia* (Elliott) Fernald, *Cnidoscolus texanus* (Muell.-Arg.) Small, *Croton argyranthemus* Michx., *Cyperus grayioides* Mohlenbrock, *Eriogonum longifolium* Nutt., *E. multiflorum* Benth., *Froelichia floridana* (Nutt.) Moq., *Hymenopappus artemisiifolius* DC., *Matelea cynanchoides* (Engelm.) Woodson, *Mirabilis albida* (Walter) Heimrl, *Opuntia humifusa* (Raf.) Raf., *Paronychia drummondii* Torr. & A. Gray, *Pediomelum digitatum* (Nutt. ex Torr. & A. Gray) Isely, *P. hypogaeum* (Nutt. ex Torr. & A. Gray) Rydb. var. *subulatum* (Bush) J.W. Grimes, *Phlox drummondii* Hook., *Polygonella americana* (Fisch. & C.A. Mey.) Small, *P. polygama* (Vent.) Engelm. & A. Gray, *Selaginella arenicola* Underwood subsp. *riddellii* (Van Eselt.) R.M. Tryon, *Streptanthes hyacinthoides* Hook., *Talinum rugospermum* Holz., *Tetragonotheca ludoviciana* (Torr. & A. Gray) A. Gray ex Hall, *Thelesperma filifolium* (Hook.) A. Gray, *Tradescantia reverchonii* Bush, *Tragia* spp., *Yucca louisianensis* Trel., and *Zornia bracteata* J.F. Gmel.

Sorrie and Weakley (2001) identify the Carrizo Sands of Texas as one endemic center for the Atlantic and Gulf Coastal plains (see McBryde 1933 for a description of this area). While the Carrizo Formation is a narrow band running from the Rio Grande to northeastern Texas and then southward to eastern Texas and has xeric sandylands scattered throughout, xeric sandylands are not confined to this formation but occur virtually throughout the WGCP in both pineywoods and post oak savanna in Oklahoma, Arkansas, Louisiana, and Texas as shown by the distribution of species fidel to this community as discussed by MacRoberts et al. (2002). In that study, in order to develop an objective idea of the distribution of xeric sandylands, we chose 42 fidel species from the total list of species occurring in this community and mapped these by county and parish over their ranges (Fig. 2) (see also McBryde 1933; Drawe et al. 1978; Ajilvsgi 1979; Marietta & Nixon 1983; Matos & Rudolph 1985; Bridges & Orzell 1989; Ward & Nixon 1992; Harcombe et al. 1993; MacRoberts & MacRoberts 1994, 1995, 1996; Hoagland 2000).

While widespread, xeric sandylands are not a dominant community across the WGCP but are generally found in relatively small patches. At the time of European settlement it has been estimated that xeric sandylands accounted for less than one percent of western Louisiana (Louisiana Natural Heritage Program 1993) and, although there are no published figures, probably no more than this in either Oklahoma or Arkansas. In Texas, especially along the Carrizo for-

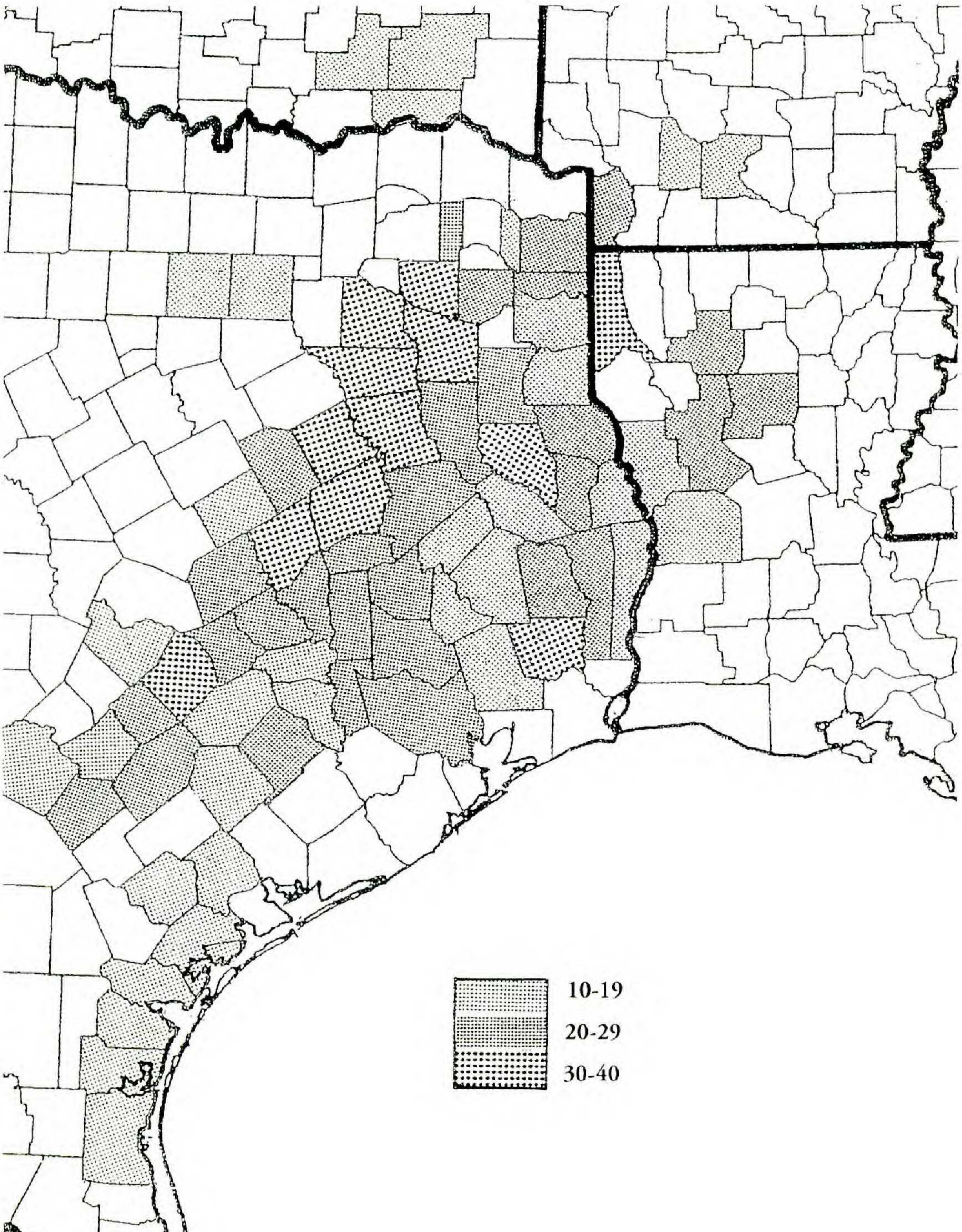

FIG. 2. Xeric sandyland species distribution. Key = number of species in sample list of 42 species located in each county either by personal inspection, herbarium searches, or literature (see MacRoberts et al. 2002 for further explanation).

mation (McBryde 1933), xeric sandylands were common, but for the whole of the region this community is unlikely to have amounted to more than five percent of the area.

While there appears to be disagreement among palynologists concerning short-term climatic events in the southeast in general and the WGCP in particular during glacial and post-glacial times as to whether or not there were south Texas and Mexican refugia (Martin & Harrell 1957; Ellis et al. 1995; Schmidtling & Hipkins 1998), the major long-term patterns are relatively clear (Bryant 1977; Watts 1980; Bryant & Holloway 1985; Webb 1988; Webb et al. 1993; Delcourt et al. 1993; Delcourt & Delcourt 1993, 2000; Bousman 1998). The picture that emerges supports the thesis presented here: xeric sandylands (open post-oak savannas and woodlands on sandy soils) were present as a community type within the WGCP since the last glaciation. We know that coarse sands necessary for the physical development of xeric habitats were present since the Eocene (McBryde 1933; Sorrie & Weakley 2001 and references therein). Prone to frequent water deficits and nutrient limitations, these soils undoubtedly have always dramatically affected vegetation structure and composition, which probably explains why percent sand present in surface soils of the Coastal Plain is a key determinant of vegetation patterns throughout this area (McBryde 1933; Harcombe et al. 1993; Peet & Allard 1993; Christensen 2000). We also know from pollen counts from dozens of bogs along the western edge of the WGCP (unfortunately the only area of east Texas with lengthy pollen records) that oaks and grasses dominated after the last glaciation (Bryant 1977; Bryant & Holloway 1985; Holloway et al. 1987). The prehistoric landscape that is revealed is one that is not dissimilar to that seen in the region today: oak-dominated sandy "savannas" and hilltops that act as reservoirs for water that feeds the adjacent seeps, marshes, streams, and peat bogs of the area (McBryde 1993; MacRoberts & MacRoberts 1998, MacRoberts et al. 2002). Unfortunately, palynology is seldom precise to species; our hypothesis would be that oaks were probably those of dryer habitat: *Quercus stellata* and *Q. incana*, and that the herbaceous vegetation included, in part, the evolving endemics described here. After all, the peat bog habitats that contain the continuous pollen profiles extending back thousands of years still exist (see MacRoberts & MacRoberts 1998; Potzger & Tharp 1947; Graham & Heimsch 1960; Bryant 1977; Holloway et al. 1987 for pollen analyses of east-central Texas bogs).

Additionally, the Mississippi River/Embayment has been a migration barrier since the Eocene (Rock 1957; Blair 1958; Sorrie & Weakley 2001). Many of the similarities between east and west have come about in the last 6000 years as the climates have approximated one another. Sandylands of the WGCP retain a distinctive flora rich in endemic and near-endemic taxa, which express more clearly than other communities in the region a long and distinctive phylogenetic history. The flora of many WGCP xeric sandylands has been enriched by the addition of taxa more widespread in the Coastal Plain. In contrast, xeric sandylands along the western drier boundary of the WGCP appear to retain a greater percentage of taxa locally characteristic of the region and with a relatively longer affiliation with it (McBryde 1933).

Our data on endemism coupled with palynological and climatic data strongly suggest that communities analogous, if not homologous, to xeric sandylands may have been a significant component of the WGCP since the last glaciation and perhaps earlier. Open oak-hickory woodlands and savannas with a rich herbaceous layer and many openings may have been the characteristic landscape over broad areas; perhaps moving south during glacial advances and north again with their retreat.

We suggest that the WGCP should no longer be overlooked as a distinct and critical region of endemism within the Coastal Plain. It may be more meaningful to look upon it as a dynamic entity with an independent and, to a certain extent, isolated ecological and biological history.

APPENDIX 1

Endemics (E) and near-endemics (NE) of the West Gulf Coastal Plain. Nomenclature follows Kartesz and Meacham (1999) in most cases. Community (habitat) types in brackets (see Appendix 2).

AGAVACEAE

Yucca louisianensis Trel., (E) [1]

ALISMATACEAE

Sagittaria papillosa Buchenau, (NE) [6]

APIACEAE

Eryngium hookeri Walp., (NE) [9 & 13]

ASTERACEAE

Berlandiera pumila (Michx.) Nutt. var. *scabrella* G.L. Nesom & B.L. Turner, (E) [1]
Chrysopsis texana Nesom, (E) [1]
Coreopsis intermedia Sherff, (E) [1]
Echinacea sanguinea Nutt., (E) [1]
Evax candida (Torr. & A. Gray) A. Gray, (NE) [1]
Gaillardia aestivalis (Walter) H. Rock var. *winkleri* (Cory) B.L. Turner, (E) [1]
Helenium drummondii H. Rock, (E) [4]
Helianthus debilis Nutt. ssp. *silvestris* Heiser, (E) [1]
Helianthus occidentalis Riddell ssp. *plantagineus* (Torr. & A. Gray) Shinners, (NE) [1]
Hymenopappus artemisiifolius DC., (NE) [1]
Hymenopappus carrizoanus B.L. Turner, (NE) [1]
Krigia wrightii (A. Gray) K.L. Chambers ex K.J. Kim, (NE) [ ]
Lactuca hirsuta Muhl. ex Nutt. var. *albiflora* (Torr. & A. Gray) Shinners, (NE) [1]
Liatris cymosa (H. Ness) K. Schumann, (E) [7]
Liatris tenuis Shinners, (E) [2]
Oligoneuron nitidum (Torr. & A. Gray) Small, (NE) [7]
Palafoxia hookeriana Torr. & A. Gray, (E) [1]
Palafoxia reverchonii (Bush) Cory, (E) [1]
Rudbeckia maxima Nutt., (NE) [13]
Rudbeckia scabrifolia L.E. Brown, (E) [10]
Rudbeckia texana (Perdue) P. Cox & Urbatsch, (NE) [4]
Solidago ludoviciana (A. Gray) Small, (NE) [1]
Symphyotrichum puniceum (L.) A. & D. Love var. *scabricaule* (Shinners) G.L. Nesom, (E) [4]
Tetragonotheca ludoviciana (Torr. & A. Gray) A. Gray ex Hall, (E) [1]
Thelesperma flavodiscum (Shinners) B.L. Turner, (E) [1]
Vernonia texana (A. Gray) Small, (NE) [1]

BRASSICACEAE

Leavenworthia aurea Torr. var. *texana* (Mahler) Rollins, (E) [7]
Lesquerella angustifolia (Nutt. ex Torr. & A. Gray) S. Watson, (E) [7]
Lesquerella pallida (Torr. & A. Gray) S. Watson, (E) [7]

CAMPANULACEAE

Lobelia puberula Michx. var. *pauciflora* Bush, (NE) [4]

CAPPARACEAE

Polanisia erosa (Nutt.) H.H. Iltis, (E) [1]

CARYOPHYLLACEAE

Paronychia drummondii Torr. & A. Gray, (E) [1]

Paronychia setacea Torr. & A. Gray, (NE) [1]
Silene subciliata B.L. Robins, (E) [2]

COMMELINACEAE
Tradescantia reverchonii Bush, (NE) [1]
Tradescantia subacaulis Bush, (E) [1]

CUSCUTACEAE
Cuscuta gronovii Willd. ex J.A. Schultes var. *calyptrata* Engelm., (E) [11]

CYPERACEAE
Fuirena bushii Kral, (NE) [4]
Rhynchospora glomerata (L.) Vahl. var. *angusta* Gale, (NE) [4,10]

EUPHORBIACEAE
Euphorbia bicolor Engelm. & A. Gray, (NE) [13]

FABACEAE
Amorpha paniculata Torr. & A. Gray, (E) [4]
Astragalus distortus Torr. & A. Gray var. *engelmannii* (E. Sheld.) M.E. Jones, (E) [1]
Astragalus leptocarpus Torr. & A. Gray, (NE) [1]
Astragalus soxmaniorum Lundell, (E) [1]
Baptisia bracteata Muhl. ex Elliott var. *laevicaulis* (A. Gray ex W. Canby) Isely, (NE) [2,13]
Baptisia nuttalliana Small, (NE) [1]
Dalea phleoides (Torr. & A. Gray) Shinners var. *phleoides*, (NE) [1]
Dalea villosa (Nutt.) Spreng var. *grisea* (Torr. & A. Gray) Barneby, (E) [1]
Mimosa hystricina (Small) B.L. Turner, (NE) [1]
Pediomelum hypogaeum (Nutt. ex Torr. & A. Gray) Rydb. var. *subulatum* (Bush) J.W. Grimes, (NE) [1]
Trifolium amphianthum Torr. & A. Gray, (NE) [2,13]
Trifolium bejariense Moric., (E) [1]

GENTIANACEAE
Bartonia texana Correll, (E) [10]

HYDROPHYLLACEAE
Nemophila phacelioides Nutt., (NE) [9]
Phacelia glabra Nutt., (NE) [13]

IRIDACEAE
Iris hexagona Walter var. *flexicaulis* (Small) R. Foster, (NE) [6]
Sisyrinchium sagittiferum Bicknell, (E) [4]

LAMIACEAE
Brazoria truncata (Benth.) Engelm. & A. Gray var. *pulcherrima* (Lundell) M.W. Turner, (E) [1]
Brazoria truncata (Benth.) Engelm. & A. Gray var. *truncata*, (NE) [1]
Monarda lindheimeri Engelm. & A. Gray ex A. Gray, (E) [5,13]
Monarda viridissima Correll, (E) [1]
Physostegia digitalis Small, (E) [2]
Physostegia longisepala Cantino, (E) [4,13]
Physostegia pulchella Lundell, (NE) [11]
Rhododon ciliatus (Benth.) Epling, (E) [1]
Scutellaria cardiophylla Engelm. & A. Gray, (E) [1]

LILIACEAE
Trillium gracile J.D. Freeman, (E) [8]
Trillium texanum Buckley, (E) [10]

MALVACEAE
Hibiscus dasycalyx Blake & Shiller, (E) [11]

MORACEAE
Maclura pomifera (Raf.) C.K. Schneid., (E) [11]

NYCTAGINACEAE
Abronia macrocarpa L. Galloway, (E) [1]

ONAGRACEAE
Oenothera heterophylla Spach ssp. *heterophylla*, (NE) [1]

ORCHIDACEAE
Spiranthes parksii Correll, (E) [7]

PAPAVERACEAE
Argemone albiflora Hornem. ssp. *texana* G.B. Ownbey, (NE) [1]

POACEAE
Panicum brachyanthum Steud., (NE) [4]
Sporobolus silveanus Swallen, (E) [7]

POLEMONIACEAE
Phlox cuspidata Scheele, (NE) [ ]
Phlox drummondii Hook. var. *drummondii*, (NE) [1]
Phlox nivalis Lodd. ex Sweet ssp. *texensis* Lundell, (E) [1]

POLYGONACEAE
Eriogonum longifolium Nutt. var. *plantaginium* Engelm. & A. Gray, (E) [1]
Eriogonum multiflorum Benth., (NE) [1]
Polygonella parksii Cory, (E) [1]

RANUNCULACEAE
Delphinium carolinianum Walter ssp. *vimineum* (D. Don) M.J. Warnock, (NE) [1]
Thalictrum arkansanum Boivin, (NE) [11]
Thalictrum texanum (A. Gray) Small, (E) [11]

ROSACEAE
Crataegus nananixonii Phipps & R. O'Kennon, (E) [1]

Crataegus warneri Sarg., (E) [1]

SCROPHULARIACEAE

Agalinis caddoensis Pennell, (E) [ ]
Agalinis navasotensis M. Dubrule & J. Canne-Hilliker, (E) [7]
Gratiola flava Leavenw., (NE) [7]
Penstemon murrayanus Hook., (NE) [1]

SOLANACEAE

Physalis mollis Nutt.var. *variovestita* (Waterfall) Sullivan, (NE) [1]

VALERIANACEAE

Valerianella florifera Shinners, (NE) [1]

APPENDIX 2

Community classification of West Gulf Coastal Plain (from Turner et al. 1999; The Nature Conservancy [TNC] designations in brackets [Weakley et al. 1999]).

1. Xeric sandylands. Grossarenic dry uplands (*Tragia* group). As a modification of this type we emphasize the xeric conditions, notably areas referred to as xeric sandylands and Post Oak-Blue Jack Oak Savanna.[TNC 305 and 320 in part].
2. Upland pine savanna, mixed woodlands. Arenic dry upland (*Schizachyrium* group). [TNC 305 and 307 in part].
3. Loamy dry-mesic uplands (*Schizachyrium*, *Callicarpa*, and *Chasmanthium* groups). We modify this entry to exclude communities where *Drosera* group (see below) dominates and place them with the next entry. [TNC 307 in part].
4. Bogs, wet pine savannas. Sandy/loamy wet herbaceous seeps and wetland pine savannas (*Drosera* group). [TNC 330 and 347].
5. Calcareous forest. Clayey dry mesic upland (*Chasmanthium* group). [TNC 375 in part].
6. Mayhaw pond. Clayey wet upland depression (*Justicia* group). [TNC 340].
7. Barrens, glades, and weches barrens (*Bigelowia*, *Callirhoe*, *Dalea* groups). Open, herb-dominated areas on bedrock exposures. [TNC 350].
8. Beech slopes. Mesic lower slopes and terraces (*Callicarpa* and *Mitchella* groups). [TNC 308].
9. Stream course. Loamy mesic stream bottom (*Mitchella* and *Arisaema* groups) and loamy wet-mesic stream bottoms (*Bignonia* and *Justicia* groups). [TNC 365 in part]
10. Baygall. Loamy wet forested seeps (*Osmunda* group). [TNC 360].
11. Floodplain, bottomland hardwood/river bottom communities; includes swamps (*Callicarpa*, *Bignonia*, *Justicia*, and *Ceratophyllum* groups). This combines Turner et al.(1999) community types 12–15. [TNC 385].
12. Open ponds and emergent marshes (not in Turner et al. 1999). [TNC 345].
13. Prairies (not in Turner et al. 1999). [TNC 375 in part].

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REFERENCES

Ajilvsgi, G. 1979. Wild flowers of the Big Thicket. Texas A. & M. Press, College Station.

Blair, W.F. 1958. Distributional patterns of vertebrates in the southern United States in relation to past and present environments. In: C.L. Hubbs, ed. Zoogeography. Publ. 51. American Association for the Advancement of Science. Pp. 433–468.

Bousman, C.B. 1998. Paleoenvironmental change in central Texas: the palynological evidence. Plains Anthropologist 43:201–219.

Bridges, E.L. and S.L. Orzell. 1987. Further additions and noteworthy collections in the flora of Arkansas, with historical, ecological, and phytogeographic notes. Phytologia 64:81–144.

Bridges, E.L. and S.L. Orzell. 1989. Longleaf pine communities of the West Gulf Coastal Plain. Natural Areas Journal 9:246–263.

Bryant, V.M. 1977. A 16,000 year pollen record of vegetational change in central Texas. Palynology 1:143–156.

Bryant, V.M. and R.G. Holloway. 1985. A late-quaternary paleoenvironmental record in Texas: An overview of the pollen evidence. In: V.M. Bryant and R.G. Holloway, eds. Pollen records of late-quaternary North American sediments. AASP Foundation, Washington, D.C., Pp. 39–70.

Christensen, N.L. 2000. Vegetation of the southeastern Coastal Plain. In: M.G. Barbour and W.D. Billings, eds. North American terrestrial vegetation. Cambridge Univ. Press. New York. Pp. 397–448.

Correll, D.S. and M.C. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner.

Delcourt, P.A. and H.R. Delcourt. 1993. Paleoclimates, paleovegetation, and paleofloras during the late Quaternary. In: Flora of North America Editorial Committee, eds. Flora of North America. Vol. 1. Oxford Univ. Press, New York. Pp 71–94.

Delcourt, H.R. and P.A. Delcourt. 2000. Eastern deciduous forests. In: M.G. Barbour and W.D. Billings, eds. North American terrestrial vegetation. Cambridge Univeristy Press. New York. Pp. 358–395.

Delcourt, P.A., H.R. Delcourt, D.F. Morse, and P.A. Morse. 1993. History, evolution, and organization of vegetation and human culture. In: W.H. Martin, S.G. Boyce, and A.C. Echternacht, eds. Biodiversity of the southeastern United States: lowland terrestrial communities. John Wiley, New York. Pp. 47–80.

Diamond, D.D., D.H. Riskind, and S.L. Orzell. 1987. A framework for plant community classification and conservation in Texas. Texas J. Sci. 39:203–221.

Diggs, G.M., B.L. Lipscomb, and R.J. O'Kennon. 1999. Illustrated flora of north central Texas. Sida, Bot. Misc. 16:1–1626.

Drawe, D.L., A.D. Chamrad, and T.W. Box. 1978. Plant communities of the Welder Wildlife Refuge. Contr. 5, Ser. B. Welder Wildlife Foundation, Sinton.

Ellis, L.W., G.L. Ellis, and C.D. Frederick. 1995. Implications of environmental diversity in the central Texas archaeological region. Bull. Texas Archaeological Soc. 66:401–426.

Estill, J.C. and M.B. Cruzan. 2001. Phytogeography of rare plant species endemic to the southeastern United States. Castanea 66:3–23.

Fenneman, N.M. 1938. Physiography of eastern United States. McGraw Hill, New York.

Foti, T., X. Li, M. Blaney, and K.G. Smith. 1994. A classification system for the natural vegetation of Arkansas. Proc. Arkansas Acad. Sci. 48:50–62.

Graham, A. and C. Heimsch. 1960. Pollen studies of some Texas peat deposits. Ecology 41:751–763.

HARCOMBE, P.A., J.S. GLITZENSTEIN, R.G. KNOX, S.L. ORZELL, and E.L. BRIDGES. 1993. Vegetation of the longleaf pine region of the west gulf coastal plain. Proc. Tall Timbers Fire Ecology Conf. 18:83–104.

HATCH, S.L., K.N. GANDHI, and L.E. BROWN. 1990. Checklist of the vascular plants of Texas. Texas Agricultural Experimental Station, College Station.

HOAGLAND, B. 2000. The vegetation of Oklahoma: a classification for landscape mapping and conservation planning. Southw. Naturalist 45:385–420.

HOLLOWAY, R.C., L.M. RAAB, and R. STUCKENRATH. 1987. Pollen analysis of late-Holocene sediments from a central Texas bog. Texas J. Sci. 39:71–79.

ISELY, D. 1990. Vascular flora of the southeastern United States. Leguminosae. Univ. North Carolina Press. Chapel Hill.

JONES, F.B. 1977. Flora of the Texas coastal bend. Mission Press, Corpus Christi.

JONES, S.D, J.K. WIPFF, and P.M. MONTGOMERY. 1997. Vascular plants of Texas. Univ. Texas Press, Austin.

KARTESZ, J.T. and C.A. MEACHAM. 1999. Synthesis of North American flora. Version 1.0. North Carolina Botanical Garden. Chapel Hill.

LOUISIANA NATURAL HERITAGE PROGRAM. 1993. Estimated presettlement and current acres of natural plant communities in Louisiana. Unpublished report. Louisiana Dept. Fish and Wildlife, Baton Rouge.

LOUISIANA NATURAL HERITAGE PROGRAM. 1998. Natural plant communites of Louisiana. Unpublished report. Louisiana Dept. Fish and Wildlife, Baton Rouge.

LOUISIANA NATURAL HERITAGE PROGRAM. 1999. Rare plant species of Louisiana. Unpublished report. Louisiana Dept. Fish and Wildlife, Baton Rouge.

MACROBERTS, D.T. 1984. The vascular plants of Louisiana. Bull. Mus. Life Sci. 6:1–165.

MACROBERTS, D.T. 1989. A documented checklist and atlas of the vascular flora of Louisiana. Bull. Mus. Life Sci. 7–9:1–756.

MACROBERTS, B.R. and M.H. MACROBERTS. 1994. Floristics of a xeric sandyland in western Louisiana. Phytologia 77:414–424.

MACROBERTS, B.R. and M.H. MACROBERTS. 1995. Floristics of xeric sandhills in northwestern Louisiana. Phytologia 79:123–131.

MACROBERTS, B.R. and M.H. MACROBERTS. 1996. Floristics of xeric sandhills in east Texas. Phytologia 80:1–7.

MACROBERTS, B.R. and M.H. MACROBERTS. 1998. Floristics of muck bogs in east central Texas. Phytologia 85:61–73.

MACROBERTS, M.H., B.R. MACROBERTS, and J.C. CATHEY. 2002. Floristics of xeric sandylands in the post oak savanna region of east Texas. Sida 20:373–386.

MARIETTA, K.L. and E.S. NIXON. 1983. Vegetational analysis of a post oak-black hickory community in eastern Texas. Texas J. Sci. 35:197–20.

MARTIN, P.S. and B.E. HARRELL. 1957. The pleistocene history of temperate biotas in Mexico and eastern United States. Ecology 38:468–480.

MATOS, J.A. and D.C. RUDOLPH. 1985. The vegetation of the Roy E. Larsen Sandylands Sanctuary in the Big Thicket of Texas. Castanea 50:228–249.

McBryde, J.B. 1933. The vegetation and habitat factors of the Carrizo sands. Ecol. Monogr. 3:247–297.

Nesom, G.L. 1997. The status of *Aster scabricaulis* (Asteraceae: Astereae), an endemic of the gulf coastal plain. Phytologia 82:300–315.

Nixon, E.S. and J.G. Kell. 1993. Ferns and herbaceous flowering plants of East Texas. Privately Published.

Peet, R.K. and D.J. Allard. 1993. Longleaf pine vegetation of the southern Atlantic and eastern gulf coastal regions: a preliminary classification. Proc. Tall Timbers Fire Ecology Conf. 18:45–81.

Potzger, J.E. and B.C. Tharp. 1947. Pollen profile from a Texas bog. Ecology 28:274–279.

Poole, J.M. and D.H. Riskind. 1987. Endangered, threatened, or protected native plants of Texas. Texas Parks and Wildlife, Austin.

Ricketts, T.H., E. Dinerstein, D.M. Olson, C.J. Loucks. W. Eichbaum, D. DellaSala, K. Kavanagh, P. Hedao, P.T. Hurley, K.M. Carney, R. Abell and S. Walters. 1999. Terrestrial ecoregions of North America. Island Press. Washington, D.C.

Rock, H.F.L. 1957. A revision of the vernal species of *Helenium* (Compositae). Rhodora 59:137–216.

Smith, E.B. 1988. An atlas and annotated list of the vascular plants of Arkansas. Privately Printed, Fayetteville.

Schmidtling, R.C. and V. Hipkins. 1998. Genetic diversity in longleaf pine (*Pinus palustris*): influence of historical and prehistoric events. Canad. J. Forest Res. 28:1135–1145.

Sorrie, B.A. and A.S. Weakley 2001. Coastal plain plant endemics: phytogeographic patterns. Castanea 66:50–82.

Takhtajan, A. 1986. Floristic regions of the World. University of California Press, Berkeley.

Taylor, R.J. and C.E.S. Taylor. 1989. An annotated list of the ferns, fern allies, gymnosperms and flowering plants of Oklahoma. Southeastern Oklahoma State University, Durant.

TAMU. Texas A. & M. Herbarium. www.csdl.tamu.edu/FLORA/tracy/main1.html.

Texas Natural Heritage Program. 1995a. Special plant list. Texas Parks and Wildlife Department, Austin.

Texas Natural Heritage Program. 1995b. Plant communities of Texas. Texas Parks and Wildlife Department, Austin.

Texas Organization for Endangered Species. 1992. Endangered, threatened, and watch list of natural communities of Texas. Austin.

Texas Organization for Endangered Species. 1993. Endangered, threatened, and watch list of Texas plants. Publ. 9. Austin.

Thomas, R.D. and C.M. Allen. 1993–1998. Atlas of the vascular flora of Louisiana. Louisiana Department of Wildlife and Fisheries, Baton Rouge.

Turner, B.L. 1995. Synoptical study of *Rhododon* (Lamiaceae). Phytologia 78:448–451.

Turner, B.L. in press. Atlas of Texas flora. Sida, Bot. Misc.

Turner, M.W. 1996. Systematic study of the genus *Brazoria* (Lamiaceae) and *Warnockia* (Lamiaceae), a new genus from Texas. Pl. Syst. Evol. 203:65–82.

Turner, R.L., J.E. Van Kley, L.S. Smith, and R.E. Evans. 1999. Ecological classification of the national forests and adjacent areas of the West Gulf Coastal Plain. The Nature Conservancy, Nacogdoches.

Van Kley, J.E. 1999a. The vegetation of the Kisatchie sandstone hills, Louisiana. Castanea 64:64–80.

Van Kley, J.E. 1999b. The vegetation of the high terrace rolling uplands, Louisiana. Castanea 64:318–336.

Walker, J. 1993. Rare vascular plant taxa associated with the longleaf pine ecosystem: patterns in taxonomy and ecology. Proc. Tall Timbers Fire Ecology Conf. 18:105–125.

Ward, J.R. and E.S. Nixon. 1992. Woody vegetation of the dry, sandy uplands of eastern Texas. Texas J. Sci. 44:283–294.

Watts, W.A. 1980. The late quaternary vegetation history of the southeastern United States. Ann. Rev. Ecol. Syst. 11:287–409.

Weakley, A.S., K.D. Patterson, S. Landaal, M. Pyne, and others (compilers). 1999. International classification of ecological communities: terrestial vegetation of the southeastern United States. The Nature Conservancy, Chapel Hill.

Webb, T. 1988. Eastern North America. In: B. Huntley and T. Webb, eds. Vegetation history. Kluwer, Amsterdam. Pp.385–414.

Webb, T., P.J. Bartlein, S.P. Harrison, and K.H. Anderson. 1993. Vegetation, lake levels, and climate in eastern North America for the past 18,000 years. In: H.E. Wright, ed. Global climates since the last glacial maximum. Univ. Minnesota Press, Saint Paul. Pp. 415–467.